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Abstract: Aquatic biodiversity in rivers and streams is threatened in many regions worldwide. As biodiversity loss has severe consequences on ecosystem functioning, it is important to understand the causes of decline and to predict biodiversity in space and time. In order to achieve this, the identification of the driving factors and the appropriate choice of indicator groups are needed. We developed a spatially explicit habitat distribution model for aquatic macroinvertebrates in Swiss watercourse networks using national biodiversity monitoring data from 410 randomly selected sampling sites. We specifically looked at two worldwide frequently used macroinvertebrate indicator groups. Using generalized linear models, we related firstly species richness of mayfly, stonefly and caddisfly (Ephemeroptera, Plecoptera, Trichoptera; EPT) and secondly richness of all macroinvertebrate families and higher-order taxa (macroinvertebrate family richness) to 38 nationwide available environmental variables. We then predicted richness of both indicator groups at the landscape scale, providing the first nationwide prediction of EPT species and macroinvertebrate family richness. Consistent with previous work, we found that variables describing land use and topology were most important for explaining richness at the landscape level. However, the two indicator groups showed opposing patterns of richness and a different sensitivity to land-use variables. This indicates that the sole use of one of these groups may be misleading with respect to water quality assessments and to the identification of overall diversity hotspots. We conclude that commonly used richness patterns derived from aggregated groups, such as family-level macroinvertebrate richness, may be less appropriate for conservation strategies.

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Landscape level predictions of diversity in river networks reveal opposing patterns for different groups of macroinvertebrates

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Abstract

Aquatic biodiversity in rivers and streams is threatened in many regions worldwide. As biodiversity loss has severe consequences on ecosystem functioning, it is important to understand the causes of decline and to predict biodiversity in space and time. In order to achieve this, the identification of the driving factors and the appropriate choice of indicator groups is needed. We developed a spatially explicit habitat distribution model for aquatic macroinvertebrates in Swiss watercourse networks using national biodiversity monitoring data from 410 randomly selected sampling sites. We specifically looked at two worldwide frequently used macroinvertebrate indicator groups. Using generalized linear models, we related firstly species richness of mayfly, stonefly, and caddisfly (Ephemeroptera, Plecoptera, Trichoptera; EPT) and secondly richness of all macroinvertebrate families and higher order taxa (macroinvertebrate family richness) to 38 nationwide available environmental variables. We then predicted richness of both indicator groups at the landscape scale, providing the first nationwide prediction of EPT species and macroinvertebrate family richness. Consistent with previous work, we found that variables describing land-use and topology were most important for explaining richness at the landscape level. However, the two indicator groups showed opposing patterns of richness and a different sensitivity to land-use variables. This indicates that the sole use of one of these groups may be misleading with respect to water quality assessments and to the identification of overall diversity hotspots. We conclude that commonly used richness patterns derived from aggregated groups, such as family level macroinvertebrate richness, may be less appropriate for conservation strategies.

Key words: Biodiversity, dendritic networks, habitat modeling, environmental niche modeling, landscape-scale, up-scaling.

Introduction

The distribution of biodiversity is typically highly spatially heterogeneous (Clarke et al. 2008). According to the metacommunity concept, the spatial distribution of taxa is shaped by the interaction between environmental factors (environmental niche) and spatial patterns (dispersal; Holyoak et al. 2005). The application of this concept is especially important in riverine ecosystems (e.g., Brown et al. 2011, Altermatt 2013, Carrara et al. 2014, Mari et al. 2014, Seymour et al. 2015), which have a characteristic dendritic network structure, to which environmental factors are inherently linked. While in the past environmental variables have been cited as primary determinants of taxa richness distribution (for reviews see Clarke et al. 2008 and Altermatt 2013), the relative importance of these determinants is now thought to vary across communities and regions (e.g., Lin et al. 2013) and to depend on the scale of observation (e.g., Seymour et al. 2016).

Changes in taxa richness alter ecosystem processes and affect the resistance of ecosystems to environmental changes (Chapin et al. 2000). Hence, improving the understanding of taxa richness distribution is important, especially with regard to the multifaceted anthropogenic impacts on taxa richness distribution (e.g., O'Connor et al. 2012). Currently observed environmental changes, such as land-use change, pollution or climate change, have an especially large impact on freshwater taxa richness distribution. 65% of the global watercourse habitats are threatened (Vörösmarty et al. 2010) and freshwater habitats have experienced a far greater decline than the most affected terrestrial habitats (Dudgeon et al. 2006). Freshwater ecosystems are particularly fragile because the dispersion of organisms is limited. Artificial structures fragment watercourses and terrestrial land-use alters the biogeochemical freshwater dynamics via the hydrological cycle at the landscape level (Allan, 2004). Given that freshwater supports almost 6% of all described species, despite only covering 0.8% (Dudgeon et al. 2006) of the earth's surface,

it is important to understand the state of biodiversity and the possible causes of biodiversity decline.

Watercourse macroinvertebrates (hereafter referred to as macroinvertebrates) are of key interest with respect to biodiversity patterns in riverine ecosystems (e.g., Heino et al. 2015) and they are often used as bioindicators. Their sampling and identification is relatively easy, their sensitivity and generally low mobility make them vulnerable to unfavorable local environments and their role in the aquatic food web is vital (e.g., Tachet 2010). Most studies on biodiversity or water quality assessments investigate macroinvertebrates either at family, genus or species richness level (e.g., Astorga et al. 2012, Grönroos & Heino 2012, Altermatt et al. 2013, Tonkin 2014, Heino et al. 2015). Family or genus richness level of macroinvertebrates is commonly used as its application is simple and as it requires relatively low taxonomic skills (e.g., Bouchard 2004, Tachet 2010). It is also the standard of many governmental richness assessments (e.g., indice biologique global normalisé IBGN; Tachet 2010). Assessments at the species richness level are also widely used, but generally focus on a few macroinvertebrate orders, such as Ephemeroptera, Plecoptera, Trichoptera (often summarized as EPT), or Odonata (for a meta-analysis that uses this kind of data see e.g., Heino et al. 2015). The identification to the species level is less commonly used than the identification to a higher taxonomic level. This is mostly attributed to the lack of appropriate identification tools and/or the lack of personnel or expertise needed for the identification. It is often assumed that the insights from one macroinvertebrate group (e.g., species level of EPT) can be transferred to other groups of macroinvertebrates (e.g., macroinvertebrate family level) (e.g., Tachet 2010).

Nowadays, advances in statistics and available GIS data and methods (Guisan & Zimmermann 2000, Guisan & Thuiller 2005) allow the inclusion of many environmental variables at the landscape level. This substantially improves taxa habitat distribution

models. A series of previous studies in the river Rhine catchment in Switzerland found that spatial patterns explain most of the variation in community composition, while environmental variables and their interaction with spatial patterns explained less (Altermatt et al. 2013, Seymour et al. 2016). However, these studies only used a subset of available environmental variables and the overall amount of variation explained in these models was not satisfactory (~20%) for predicting spatial heterogeneity of EPT and macroinvertebrate family richness at the landscape level.

In this study, we carried out a spatially explicit nationwide macroinvertebrate habitat distribution model for the EPT species richness and the macroinvertebrate family and higher order taxa richness in Swiss watercourse networks, with the help of regression analyses. We used an extensive set of environmental variables (including hydraulic conditions, land use variables, and topological variables; see Table 1 for the full list of variables) to firstly predict taxa richness at the landscape level, and to secondly compare the diversity patterns among these two major macroinvertebrate indicator groups. The latter aim is important, as it clarifies if biomonitoring approaches, which use different taxa level identifications, draw the same conclusions regarding biodiversity distribution and potential biodiversity drivers.

Material and Methods

To model taxa richness-distribution, we used macroinvertebrate family richness and EPT species richness from 410 randomly selected and monitored watercourse sites within Switzerland. These sites are monitored by the nationwide federal biodiversity monitoring program (Biodiversity Monitoring Switzerland, BDM). Details regarding the study sites, sampling procedure and methodologies used in the BDM can be found in Stucki (2010) and Altermatt et al. (2013). As explanatory variables, we used 38 environmental variables

124 (Table 1), which were available nationwide at the landscape level. Firstly, we modeled
125 diversity-distributions and secondly, we predicted the nationwide richness patterns of both
126 indicator groups to 22,169 sub-catchments at the landscape level, covering all of
127 Switzerland. The modeling steps included the definition of the study areas, the selection of
128 appropriate environmental variables and the model building, selection, prediction and
129 evaluation (Figure 1).
130
131 *Response variable: diversity of macroinvertebrates*
132 In Switzerland, the BDM has monitored macroinvertebrates in watercourses at 570
133 randomly distributed sampling sites since 2009 (Stucki 2010, Altermatt et al. 2013,
134 Koordinationsstelle BDM 2014). Only wadable watercourses with a Strahler order ≥2
135 which appear on maps with a 1:25,000 scale are considered. Yearly, a distinct and random
136 subset of all sites is monitored with equal sampling effort. At the time our study was
137 carried out, data from 410 sampling sites were available (dots in Fig. 2). Each sampling
138 site consists of an area defined by the width of the stream x 10 times the width (giving the
139 length). At each site, macroinvertebrates are sampled based on well-defined procedures
140 using the kicknet method (for details see Stucki 2010, Altermatt et al. 2013). In total eight
141 samples were taken at all habitat types found within the sampling site (for details see
142 Stucki 2010) and subsequently pooled. Macroinvertebrates belonging to the orders of
143 mayfly, stonefly or caddisfly (Ephemeroptera, Plecoptera and Trichoptera; abbreviated as
144 EPT) are identified to the species level. The sum of these species per site is henceforward
145 referred to as “EPT species richness”. All other macroinvertebrates are identified to the
146 family or higher taxa level (Stucki, 2010). The sum of these higher taxa level per site is
147 henceforward referred to as “macroinvertebrate family richness”.
148

149 *Definition and use of sub-catchments*

150 To up-scale diversity patterns from the sampling site-level to the landscape level, we
151 linked sampling site diversity patterns to environmental variables that were available at the
152 landscape level. We assumed that the environmental niche is homogenous within a sub-
153 catchment unit at small scale. We thus used the nationwide available catchment datasets
154 (BAFU 2012) at the 2 km^2 scale. For this dataset many environmental variables are
155 available (Tables 1 and S1). The nationwide landscape-level prediction was carried for
156 22,169 sub-catchments covering all of Switzerland (BAFU 2012).

157

158 *Explanatory variables: environmental variables*

159 We only considered environmental variables for which nationwide landscape-level spatial
160 data were available at the resolution of our 2 km^2 sub-catchments. Many previous studies
161 primarily related macroinvertebrates to locally measured in-stream habitat features such as
162 pH or water temperature (e.g. Miserendino 2001, Aguiar et al. 2002, Heino et al. 2003). As
163 these variables are generally not available at the landscape level it is not possible to use
164 them for landscape-level predictions. We initially selected 38 environmental variables.
165 These variables are characterized by ecological relevance and previous usage in literature
166 (e.g. Richards et al. 1997, Sliva & Williams 2001, Sawyer et al. 2004, Egler et al. 2012,
167 Wahl et al. 2013, Seymour et al. 2016) (Supplement Table S1 and Fig. S7). To avoid a
168 multicollinearity problem, we had to select a subset of variables for the analysis. Firstly,
169 variables that correlated with each other ($|r| > 0.7$) were grouped (Supplement Table S2).
170 We retained the most powerful explanatory variable per correlation group considering the
171 quality of the spatial datasets and using tree models. Tree models give guidance about
172 which explanatory variables to include by indicating which explanatory variables have the
173 biggest explanatory power. Secondly, a tree model was carried out for all correlating

174 explanatory variables with the highest explanatory power and all non-correlating
175 explanatory variables (Supplement Fig. S1 and S2). We thereby ended up with a set of 11
176 variables for the EPT species and a set of 10 variables for the macroinvertebrate families,
177 which we used for the final model-building (Table 2 and 3).
178
179 *Statistical analysis: generalized linear model*
180 We conducted generalized linear models (GLMs) using Poisson error distribution.
181 To avoid over-parameterization, we only considered main effects and all two-way
182 interactions. To reduce redundant variables we used two independent model selection
183 procedures. Firstly, we used a stepwise selection method based on Akaike's Information
184 Criteria (backward stepwise selection method, in the following referred to as "step
185 model"). Secondly, we used a model shrinkage method (lasso model selection method, in
186 the following referred to as "lasso model"). The model building and selection was carried
187 out for EPT species and macroinvertebrate family richness on the basis of the 410 BDM
188 sub-catchments. We then used these models to predict the nationwide richness at the
189 landscape level. For the model evaluation we used the standard error and the residuals
190 between the mean of the lasso and the step prediction and the recorded macroinvertebrate
191 richness values.
192 All modeling steps were carried out with programmed scripts in Python (Python
193 team 2014) and R (R Core team 2014) with R packages *tree* (Ripley, 2015) and *glmnet*
194 (Friedman et al. 2010), to automate repetitive steps and ensure reproducibility.
195
196 **Results**
197 Across all watercourses in Switzerland, the average richness of EPT taxa was 15.2 (range
198 0–35) and the average richness of macroinvertebrate families was 19.8 (range 1–39; for

more details on these richness distributions, see also Altermatt et al. 2013 and Seymour et al. 2016). The environmental variables explaining EPT species richness include, from most significant to least, *proportion of forest area, proportion of green area, proportion of corn cultivation area, proportion of street area, proportion of deciduous forest relative to total forest area, proportion of carbonate rock* and *total length of watercourses* (if not specified differently, all proportions relative to total sampling catchment area; for details, see Table 2). The environmental variables explaining macroinvertebrate family richness are, from most significant to least, *proportion of green area, mean meters above sea level, proportion of forest area, proportion of building facade area, proportion of vegetable cultivated area, mean watercourse gradient, proportion of vineyard area* and *proportion of orchard area* (if not specified differently, all proportions relative to total sampling catchment area; for details, see Table 3). Although some environmental variables are significant for both macroinvertebrate indicator groups, there are substantial differences in the environmental variables contributing significantly to the explanation of the respective macroinvertebrate indicator group. Important differences between the EPT species richness and macroinvertebrate family richness models were found in related but distinct arable land-use categories (captured by *proportion of corn cultivation area* in the EPT species and by *proportion of vegetable cultivated area* in the macroinvertebrate family model) and in developed area land-use categories (*proportion of street area* for EPT species and *proportion of building facade area* for macroinvertebrate family richness, respectively). The environmental variables *proportion of forest area* and *proportion of green area*, in contrast, were important for both the EPT species and the macroinvertebrate family. For the EPT species, agriculture (*proportion of corn cultivation area*) reduced a more significant amount of deviance of the recorded macroinvertebrate richness than man-made constructions (*proportion of street area*). The opposite holds true for the

macroinvertebrate taxa: settlements (*proportion of building facade area*) reduced a more significant amount of deviance of the recorded macroinvertebrate richness than agriculture (*proportion of vegetable cultivated area*). *Meters above sea level* and *mean watercourse gradient* did not reduce a significant amount of deviance on their own, but only reduced a significant amount of deviance of the recorded EPT species richness in interactions with other variables. *Proportion of carbonate rock* and *proportion of deciduous forest relative to total forest area* reduced a significant amount of deviance for the EPT species recorded but not for the macroinvertebrate family taxa recorded.

The nationwide predictions of EPT species and macroinvertebrate richness showed highly distinct and diverging patterns (EPT species richness Fig. 2 and Supplement Fig. S3; macroinvertebrate family richness Fig. 3 and Supplement Fig. S4). The nationwide EPT species prediction maps suggest that the EPT species mostly occur in wooded and livestock farming areas at intermediate elevation (compare richness predictions in Figs. 2 and 3 with the spatial distribution of all environmental variables given in Fig. S7). Distinctly fewer EPT species occur in highly cultivated lowland areas or at high-altitude regions of the Alps. The nationwide predicted distribution of the macroinvertebrate family richness shows an opposing pattern. It is mainly driven by decreasing richness with increasing elevation. There are some exceptions to this conclusion (e.g., the “Wallis” in southern Switzerland). The Wallis is characterized by high values of the land-use variables *proportion of orchard area* and *proportion of vineyard area*. When comparing the nationwide predictions of the EPT species richness and of the macroinvertebrate family richness two observations can be made. Firstly, the nationwide EPT species predictions show a wider range of predicted values than the nationwide macroinvertebrate family richness prediction. Secondly, based on visual inspection, the predicted EPT species richness values and macroinvertebrate family richness values do not correlate spatially.

The range of the estimated standard error is larger for the macroinvertebrate family richness prediction than for the EPT species richness prediction (Fig. S5). High estimated standard errors are often found at lake inflows and outflows for both taxa groups. When comparing the individual predictions (EPT species richness and macroinvertebrate family richness with the step and lasso model respectively) with the monitored values, we found that the macroinvertebrate indicator group richness is over-predicted by the models when few macroinvertebrates are present and under-predicted by the models when numerous macroinvertebrates are present (Supplement Fig. S6).

Discussion

We here present the first nationwide prediction of the EPT species and macroinvertebrate family richness for Switzerland (Figs. 2 & 3). We find highly diverging diversity patterns and thus question the common interchangeable use of these groups as ecological indicators (e.g., Bouchard 2004, Tachet 2010). In our analysis, we only used land-use variables that are available at the landscape level. This allows the nationwide prediction of the macroinvertebrate indicator group richness at the landscape-level. Such an approach has been rarely applied before. Most studies from other regions (including major catchments in North America, Europe and Asia; e.g., Heino et al. 2003, Maloney et al. 2011, Astorga et al. 2012, Grönroos & Heino 2012, Tonkin 2014, Heino et al. 2015, Tonkin et al. 2015, but see Richards et al. 1997) have related macroinvertebrate diversity to locally measured environmental variables (see also similar studies on fish, e.g. Blanchet et al. 2012). While the latter approach allows the identification of relevant local variables, it generally prohibits landscape level predictions, which are, for example, commonly conducted for terrestrial plants or animals (Guisan & Zimmermann 2000, Guisan & Thuiller 2005). Such landscape level predictions and visualizations, however, are crucial for the planning and

274 communication of conservation strategies and management actions in freshwater
275 ecosystems, and allow to disentangle the effect of local environmental variables versus
276 network structure as drivers of diversity in dendritic networks (Altermatt 2013, Carrara et
277 al. 2014). Whereas landscape-level predictions exist at national or continental scales for
278 marine or terrestrial organisms (e.g., Guisan & Zimmermann, 2000; Tittensor et al. 2010),
279 there are very few examples for freshwater invertebrates. Moreover, they are mostly
280 restricted to a small set of taxa (e.g., amphipods or groundwater crustaceans, Altermatt et
281 al. 2014, Zagmajster et al. 2014).

282 Diversity and richness of macroinvertebrates in freshwater are, among others,
283 affected by human land use change and chemical pollution. Our up-scalable landscape-
284 level environmental variables (Table 1, Fig. S7) were chosen to closely match previously
285 identified relevant environmental variables affecting macroinvertebrates. In accordance to
286 past local-scale studies (e.g., Roy et al. 2003, Moore & Palmer 2005, Egler et al. 2012,
287 Wahl et al. 2013), the nationwide model predicted that EPT species richness is highest in
288 woodlands, followed by grasslands and pastures during our landscape-level approach. In
289 contrast to past studies, however, the model predicted the lowest EPT species richness in
290 cultivated areas (especially vine- and fruit-growing areas) and not in populated areas. This
291 suggests that pollutants from cultivated land (e.g., Wittmer et al. 2014) may be having a
292 greater effect on the EPT species richness in Switzerland than urban pollution. This
293 observation is supported by the fact that arable land variables reduce more residual
294 deviance of the recorded EPT species richness than urban site variables. In accordance, a
295 study found that a significant proportion of chemicals found in rivers can be attributed to
296 plant protection products used in agriculture (Wittmer et. al 2014). This indicates that
297 agriculture impacts water quality more than populated areas, corroborating the observed
298 and the predicted diversity patterns at the landscape level.

299 In contrast, the nationwide macroinvertebrate family richness prediction does not
300 strictly follow the land-use ranking found in literature (e.g., Heino et al. 2003, Grönroos &
301 Heino 2012) and is mainly determined by the topological variables elevation and mean
302 watercourse gradient (i.e., steepness). A pattern of highest richness at mid-elevation has
303 recently also been attributed to the topographic structure of landscapes only (Bertuzzo et
304 al. 2016). Nevertheless, the statistical results (Table 3) indicate that land-use variables
305 significantly reduce the residual deviance of the recorded macroinvertebrate family
306 richness. As the macroinvertebrate family is a conglomerate of numerous orders (Stucki
307 2010), they are characterized by a variety of different ecological niches. Thus it is likely
308 that there is a larger variance among the sensitivity of the macroinvertebrate family
309 towards land-use variables than among the EPT species. As a consequence, the effects that
310 were observed for the EPT species richness may be blurred for the macroinvertebrate
311 family richness. This might also explain why the developed area land-use variable reduces
312 more residual deviance of the recorded macroinvertebrate family species richness during
313 the BDM than the cultivated land-use variables. Different cultivated-land-use variables
314 (EPT species richness: *proportion of corn cultivation area*; macroinvertebrate family
315 richness: *proportion of vegetable cultivated area*) and developed area land-use variables
316 (EPT richness: *proportion of street area*; macroinvertebrate family richness: *proportion of*
317 *building facade area*) explained the largest amount of deviance in the response variable for
318 the EPT species richness and macroinvertebrate family taxa richness. This reinforces the
319 idea that different macroinvertebrate orders are characterized by distinct sensitivities and
320 habitat preferences.

321 The observed over- and under-predictions in the models (Supplement Fig. S6)
322 indicate that additional explanatory variables may need to be considered in the models. We
323 are aware that in-stream habitat features, such as riverbed substrate or flow rate, would

improve the model. But for a landscape-level prediction they would need to be available nationwide, which is unfortunately rarely the case. The observed macroinvertebrate richness values reflect the realized niche, while the models only considers the fundamental niche by including environmental variables. Thereby they neglect interspecific competition and predation (Wrona & Dixon 1991), and assume simplistic assumptions regarding dispersal and spatial network configuration (e.g., 2D lattice instead of dendritic networks for riverine systems; Altermatt 2013). This may explain some of the observed over- and under-prediction.

Conclusion

Understanding the relationship between environmental variables and macroinvertebrate diversity is an important milestone in understanding ecosystem processes in aquatic systems. It is the basis for evaluating potential river restoration successes (Jähnig et al. 2011, Sundermann et al. 2011). We here present the first landscape level predictions of macroinvertebrate diversity in Swiss rivers. Furthermore, we show that different land-use variables (forest, pasture, cultivated land and developed area) and topology variables (elevation and slope) have distinct impacts on different macroinvertebrate indicator groups. Specifically, we found that the distribution of the sensitive EPT species richness is clearly different from the more diverse macroinvertebrate family richness. The latter are a conglomerate of different species per family and have a much less well-defined ecological niche. We conclude that a more causal understanding of the environmental variable-macroinvertebrate indicator group richness relationship is gained when the focus is placed on a few sensitive macroinvertebrate taxa identified to the species level, than when numerous macroinvertebrate taxa are considered at the family level.

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